

RECLASSIFICATION OF *PANOPEA GENEROSA* VAR. *TAENIATA* DALL, 1918, A FOSSIL MORPHOTYPE OF *P. GLOBOSA* DALL, 1898

Ignacio Leyva-Valencia^{1*}, Brent Vadopalas², Pedro Cruz-Hernández¹,
Daniel B. Lluch-Cota¹ & Delia I. Rojas-Posadas¹

INTRODUCTION

Two extant species of geoduck clams occur on the coast of the Baja California Peninsula. *Panopea generosa* Gould, 1850, occurs from southern Alaska, U.S.A., to Punta Eugenia on the Pacific coast of the Baja California Peninsula, and *P. globosa* Dall, 1898, which was historically considered endemic to the Gulf of California. Despite their geographic proximity, *P. generosa* and *P. globosa* are not phylogenetically close (Rocha-Olivares et al., 2010). In addition, based on morphological and genetic similarity, it has been shown that *P. globosa* occurs outside the Gulf of California on the Pacific coast of the southern Baja California Peninsula in Bahía Magdalena (Leyva-Valencia, 2012; Leyva-Valencia et al., 2012).

The nomenclature of the Pacific coast species of this genus has been controversial. For example, Vadopalas et al. (2010) showed that despite distinct morphological differences between the holotypes of *P. generosa* and *P. abrupta* (Conrad, 1849), they were mistakenly synonymized in 1983. Dall first described *Panopea globosa* as a variety of *P. generosa* from a shell collected at San Felipe in the northern Gulf of California; he also described the fossil *P. solida*, from San Francisco, California (Dall, 1898). Twenty years later, Dall described a new variety of *P. generosa* – *P. generosa* var. *taeniata*, Dall, 1918 – from a fossil collected in Pleistocene marine sediments on Isla Magdalena (Fig. 1), a site directly adjacent to extant aggregations of what are now recognized as *P. globosa* in Bahía Magdalena, Baja California Sur.

The fossil record of *P. globosa* available in the paleontology collection of the San Diego Natural History Museum (SDNHM) indicates that this species was sympatric with *P. generosa* from the late Miocene to the Pleistocene in the predecessor of the Salton Sea in southern California, and fossils of both species have

been found in Puertecitos in the upper Gulf of California (Judith Smith, Smithsonian Institution, National Museum of Natural History, 2011, pers. comm.). Although the Baja California fossil record is not well characterized, *P. globosa* was present during the Pliocene and Pleistocene in the middle, southern and western coast of the Peninsula (Scott Rugh, San Diego Natural History Museum, 2010, pers. comm.; Gerardo Barba, Universidad Autónoma de Baja California Sur, 2010, pers. comm.; Judith Smith, 2011, pers. comm.), in accord with the distribution of extant aggregations.

The goal of this study was to determine whether *P. taeniata* is, as Dall described, a variety of *P. generosa*, or a fossil of *P. globosa*. The latter would suggest that the *P. globosa* distribution extended out of the Gulf of California prior to the last glacial period.

METHODS

Shell shape analysis was performed using a geometric morphometric method, as previously used to discriminate between *Panopea generosa* and *P. globosa* (Leyva-Valencia et al., 2012). Digitized images were captured at 300 dpi in JPG format (Hewlett-Packard ScanJet 2200c) of the holotypes *P. generosa* (USNM 5844), *P. globosa* (USNM 74884), *P. taeniata* (USNM 372847) and *P. solida* (USNM 3480), as well as 180 specimens of *P. globosa* from Bahía Magdalena (n = 50), San Felipe (n = 50), Puerto Peñasco (n = 50) and Guaymas (n = 30); and 204 of *P. generosa* from Alaska (n = 11), Washington (n = 55), California (n = 54) and Baja California (n = 84).

All images were imported to tpsUtil 1.44 (Rohlf, 2009). We selected outline landmarks using the fan-based method (MakeFan6 software; Sheets et al., 2006). We also selected three internal anatomical landmarks and 48

¹Centro de Investigaciones Biológicas del Noroeste, S. C., Instituto Politécnico Nacional No. 195, Col. Playa Palo de Santa Rita Sur, Apdo. Postal 128; La Paz, B.C.S. 23096, México.

²School of Aquatic Fishery Sciences, University of Washington, 1122 NE Boat St., Seattle, Washington 98105, U.S.A.

*Corresponding author: ileyvalencia@gmail.com

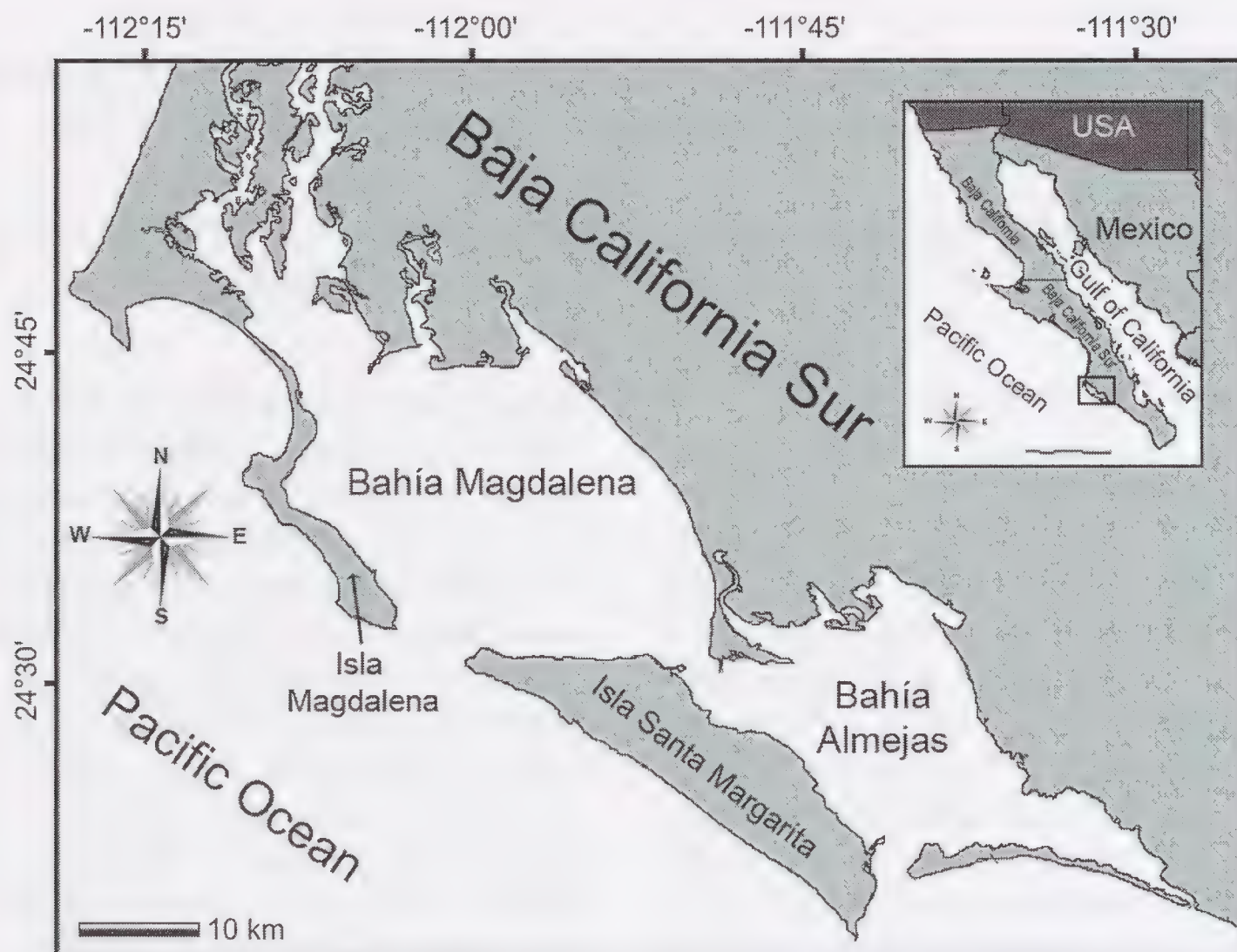


FIG. 1. Location of Isla Magdalena, collection site of *Panopea generosa* var. *taeniata* holotype.

semi-landmarks to generate two-dimensional Cartesian coordinates using tpsDig 2.12 (Rohlf, 2008). To minimize least-squares differences between landmark alignments and produce Procrustes shape coordinates, we used IMP: CoordGen6f software (Sheets et al., 2006). To accurately slide semi-landmarks along a contour to minimize the bending energy of deformation for a given specimen, we used IMP: SemiLand6 (Sheets et al., 2006). To characterize the shell outline variation between groups, we used canonical variates analysis and multivariate analysis of variance (CVA-MANOVA) in CVAGen6m (Sheets et al., 2006).

RESULTS AND DISCUSSION

The analyses of outline and internal landmarks revealed only one highly discriminant canonic variate separating *Panopea generosa* from *P. globosa*. *Panopea taeniata* was included within the *P. globosa* group, whereas *P. solida* was included within the *P. generosa* group (Fig. 2).

The shell morphology of *P. taeniata* agrees with the taxonomic characteristics of *P. globosa*. Both species have a deeper pallial sinus than *P. generosa*, and the nymph length of *P. taeniata* is shorter than in *P. generosa*. The *P.*

taeniata valve contour also shows the same inflated anterior region and narrow posterior end as *P. globosa* (Fig. 3A). On the other hand, the *P. solida* valve agrees with the general phenotype of *P. generosa*. *Panopea solida* and *P. generosa* holotypes show a hard and large nymph, with a similar pallial sinus morphology, dorsal and ventral margins with parallel growth to the shell length, a rounded anterior region and a wide posterior region (Fig. 3B). A recent morphometric study between *P. generosa* and *P. globosa* revealed great interspecific differences on anteroventral region, posterior end, pallial sinus depth and nymph length (Leyva-Valencia et al., 2012). Our results show that *P. taeniata* is not a fossil subspecies of *P. generosa*, and is hereby reclassified as a fossil morphotype of *P. globosa*.

The identification of *Panopea globosa* fossils from Isla Magdalena suggests that the extant *P. globosa* aggregation in Bahía Magdalena is ancient, at least 125,000 years old. The origin of this population is unknown, although the Pliocene to Pleistocene fossil record along of the Gulf of California and San José del Cabo Basin agree with the hypothetical migration pattern from the Gulf of California to the Bahía Magdalena area (Judith Smith, Smithsonian Institution, National Museum of Natural History, 2011, pers. comm.). Bahía Magdalena

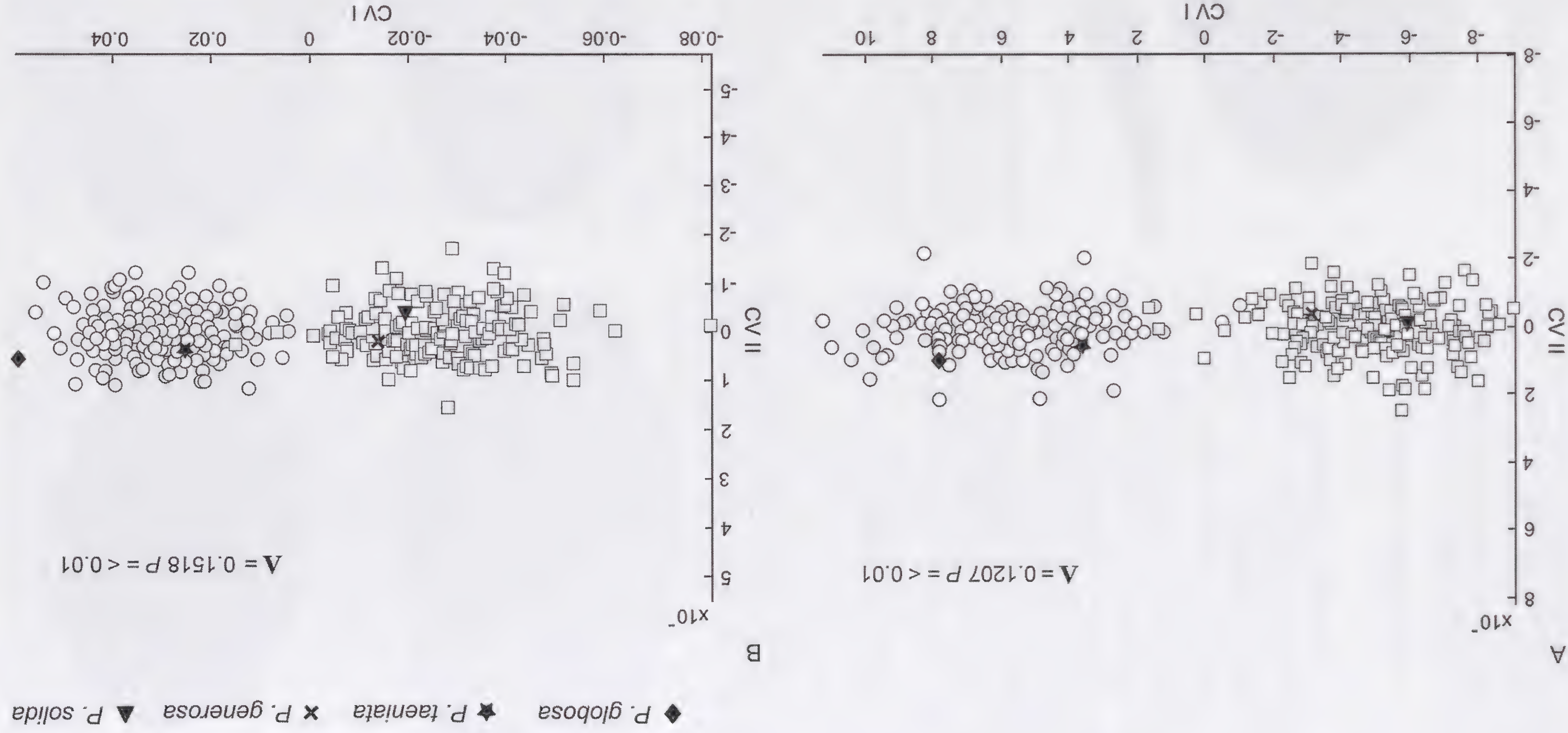


FIG. 2. CVA analyses of *Panopea generosa* (□) and *P. globosa* (O). A: Discriminate contour landmarks among *P. globosa*, *P. taeniata*, *P. generosa* and *P. solida* holotypes; B: Discriminate internal landmarks among *P. globosa*, *P. taeniata*, *P. generosa* and *P. solida* holotypes.

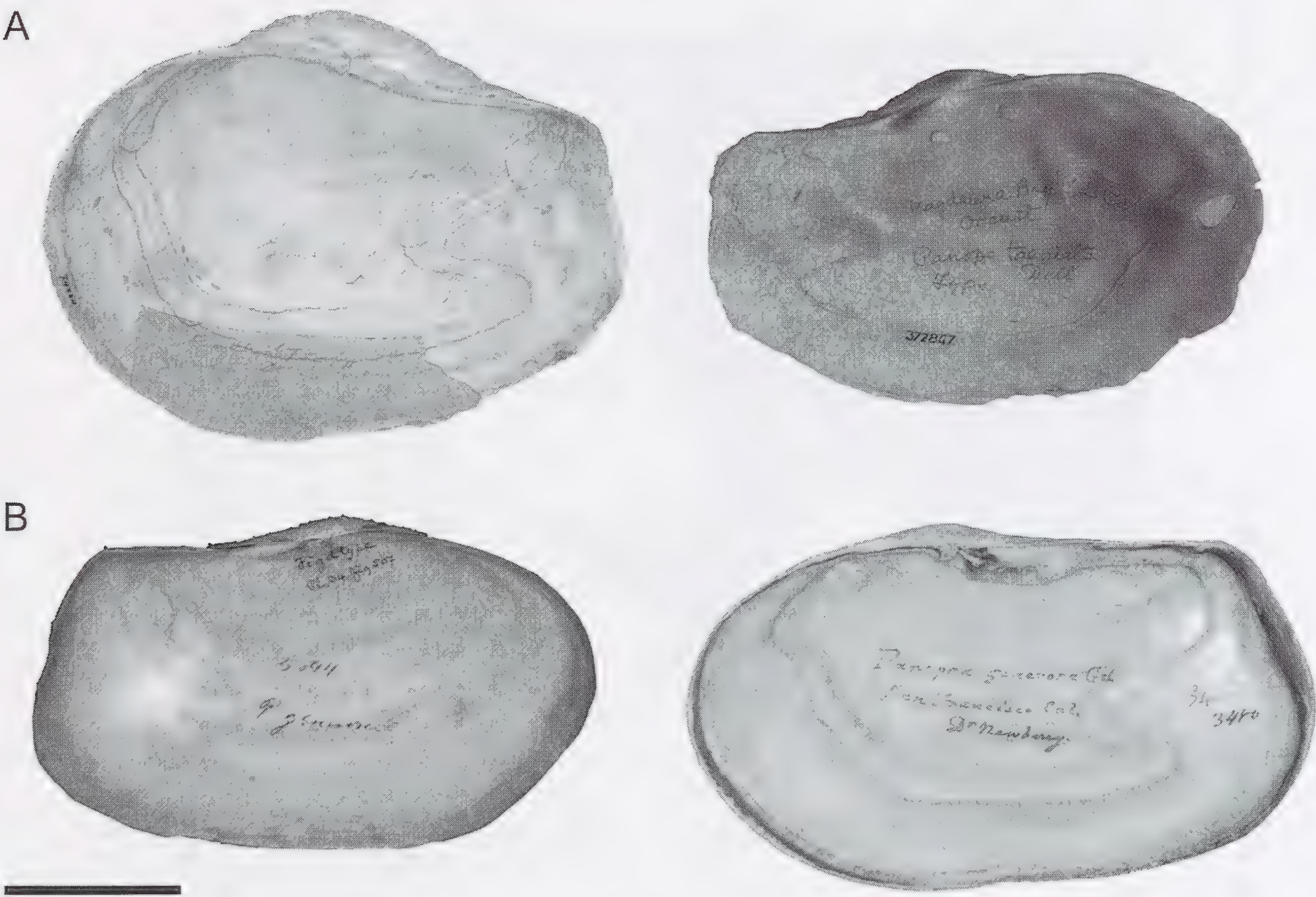


FIG. 3. Contour similarities of *Panopea* spp. A: Contour similarities between *Panopea globosa* (left) and *P. taeniata* (right). Images courtesy of Judith Smith, USNM 2012; B: Contour similarities between *P. generosa* (left) and *P. solida* (right). Images courtesy of Yolanda Villacampa, USNM 2010. Scale bar = 5 cm.

and Bahía Almejas are tectonic structural lagoons (Lankford, 1977) formed by northwest-southeast faulting along the Tosco-Abrejos fault zone around 20,000 years ago. Rising sea levels filled depressions, and the uplifted side of the fault gave rise to Isla Santa Margarita and

Isla Magdalena (Spencer & Normark, 1979; Blake et al., 1984).

Panopea taeniata fossils also have been recorded in Bahía Santa Ines, near Santa Rosalia in the central Gulf of California (Fig. 4; Durham, 1950; Libbey & Johnson, 1997). Although we cannot analyze this specimen using morphometric methods, the image permits morphologic traits to be distinguished, including a narrow posterior end, non-parallel dorsal and ventral margins, a wide anterior end as well as a short nymph. These traits are shared with *P. globosa*, and thus we conclude that this specimen was misidentified as a subspecies of *P. generosa*. In addition to the reclassification of the *P. taeniata* holotype, fossils such as that of Durham (1950) should be attributed to *P. globosa*.

ACKNOWLEDGEMENTS

Judith Terry Smith (USNM), Gerardo González Barba (UABCS) and Scott Rugh (BFSA) provided valuable paleontological information. Miguel Cordoba (CIBNOR) provided detailed editorial comments. We also thank the Yolanda



FIG. 4. Fossil of *P. generosa* var. *taeniata* from Bahía Santa Ines, Gulf of California. Image modified from Durham (1950).

Villacampa (USNM) for the holotype images. George Davis provided valuable comments and constructive criticisms to improve the manuscript. The research was funded by Consejo Nacional de Ciencia y Tecnología (CONACYT, grant 106905).

LITERATURE CITED

- BLAKE, M. C., A. S. JAVKO & T. E. MOORE, 1984, Tectonostratigraphic terranes of Magdalena Island, Baja California Sur. Pp. 183–191, in: V. A. FRIZZELL, ed., *Geology of the Baja California Peninsula*. Pacific Section, Society of Economic Paleontologists and Mineralogists, 273 pp.
- CONRAD, T. A., 1849, Fossils from northwestern America, Mollusca. Pp. 723–728 pls 17–21, in: J. D. DANA, ed., 1849. *Geology. United States Exploring Expedition. During the years 1838 ... 1842. Under the command of Charles Wilkes, U.S.N.* 10: Appendix 1.
- DALL, W. H., 1898, Contribution to the Tertiary Fauna of Florida. *Transactions of the Wagner Free Institute of Science of Philadelphia*, 3(4): 827–832.
- DALL, W. H., 1918, Pleistocene fossil of Magdalena Bay, Lower California, collected by Charles Russell Orcutt. *The Nautilus*, 32: 23–26.
- DURHAM, J. W., 1950. Megascopic paleontology and marine stratigraphy, Pt. 2 of the 1940 E.W. Scripps Cruise to the Gulf of California. *Geological Society of America Memoir*, 43: 1–216.
- GOULD, A., 1850, Shells from the U. S. Exploring Expedition. *Proceedings of the Boston Society of Natural History*, 3: 214–218.
- LANKFORD, R. R., 1977, Coastal lagoons of Mexico. Their origin and classification. Pp. 182–216, in: M. L. WILEY, ed., *Estuarine processes*. Volume II: Circulation, sediments, and transfer of material in the estuary. Academic Press, New York, 428 pp.
- LEYVA-VALENCIA, I., 2012, *Diferencias morfo-métricas en dos especies de la almeja generosa: Panopea generosa (Gould 1850) y P. globosa (Dall 1898) y filogenia molecular de cinco especies del género Panopea*. Ph.D. Thesis. Centro de Investigaciones Biológicas del Noroeste, La Paz Baja California Sur, México, 104 pp.
- LEYVA-VALENCIA, I., S. T. ÁLVAREZ-CASTAÑEDA, D. B. LLUCH-COTA, S. GONZÁLEZ-PELÁEZ, S. PÉREZ-VALENCIA, B. VADOPALAS, S. RAMÍREZ-PÉREZ & P. CRUZ-HERNÁNDEZ, 2012, Shell shape differences between two *Panopea* species and phenotypic variation among *P. globosa* aggregations using two geometric morphometrics approaches. *Malacologia*, 55(1): 1–13.
- LIBBEY, L. K. & M. JOHNSON, 1997, Upper Pleistocene rocky shores and intertidal biotas at La Playa La Palmita (Baja California Sur, Mexico). *Journal of Coastal Research*, 13: 216–225.
- ROCHA-OLIVARES, A., L. CALDERON-AGUILERA, E. A. ARAGÓN-NORIEGA, N. C. SAAVEDRA-SOTELO & V. M. MORENO-RIVERA, 2010, Genetic and morphological variation of northeast Pacific *Panopea* clams: evolutionary implications. *Journal of Shellfish Research*, 29: 327–335.
- ROHLF, J., 2008, tps Dig2. <http://life.bio.sunysb.edu/morph/index.html>
- ROHLF, J., 2009, tps Util Version 1.44. <http://life.bio.sunysb.edu/morph/soft-utility.html>
- SHEETS, D., M. ZELDITCH & D. SWIDERSKI, 2006, IMP (Integrated Morphometrics Package): <http://www.canisius.edu/~sheets/morphsoft.html>
- SPENCER, J. E. & W. R. NORMARK, 1979, Tosco-Abreojos fault zone: a Neogene transform plate boundary within the Pacific margin of southern Baja California, Mexico. *Geology*, 7: 554–557.
- VADOPALAS, B., T. PIETSCH & C. FRIEDMAN. 2010, The proper name for the geoduck: resurrection of *Panopea generosa* Gould, 1850, from the synonymy of *Panopea abrupta* (Conrad, 1849) (Bivalvia: Myoida: Hiatellidae). *Malacologia*, 52: 169–173.

Revised ms. accepted November 30, 2012